Becklesia maulnyi sp. nov.: A new cycadean species from the Lower Oxfordian (Upper Jurassic) of Écommoy (Sarthe, NW France)

Le Couls, Matthieu; Hilton, Jason; Guillocheai, François ; Morel, Nicolas; Courville, Philippe

DOI:
10.1016/j.annpal.2016.05.005

Document Version
Peer reviewed version

Citation for published version (Harvard):
Le Couls, M, Hilton, J, Guillocheai, F, Morel, N & Courville, P 2016, 'Becklesia maulnyi sp. nov.: A new cycadean species from the Lower Oxfordian (Upper Jurassic) of Écommoy (Sarthe, NW France)', *Annales de Paléontologie*. https://doi.org/10.1016/j.annpal.2016.05.005

Becklesia maulnyi sp. nov.: A new cycadean species from the Lower Oxfordian (Upper Jurassic) of Écommoy (Sarthe, NW France)

Becklesia maulnyi sp. nov. : une nouvelle espèce de cycadale de l'Oxfordien Inférieur (Jurassique supérieur) d'Écommoy (Sarthe, NO France)

Matthieu LE COULS[a]*, Jason HILTON[b], François GUILLOCHEAU[a], Nicolas MOREL[c], Philippe COURVILLE[a]

[a] UMR CNRS 6118 Géosciences, Université Rennes 1, Campus de Beaulieu, 263 avenue du général Leclerc, 35042 Rennes cedex, France.

[b] School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom.

[c] Musée Vert, 204 avenue Jean Jaurès, 72100 Le Mans, France.

*: Corresponding author: matthieu.lecouls@univ-rennes1.fr

ABSTRACT

Plant macrofossil remains of *Becklesia* Seward 1895 emend. Watson and Cusack 2005, a rare genus of extinct cycad, have been known for over a century from Great Britain and Libya. Historically the genus was poorly characterised leading to many fossil cycads that resembled *Becklesia* being placed in other genera including *Cycadites* and *Paracycas*. We describe here a new species, *B. maulnyi* sp. nov., from an exceptional and almost complete cycad specimen housed for two hundred years in the collections of the Musée Vert of Le Mans. The specimen comprises the apex of a stem bearing petiolate and pinnate leaves with thin and widely separated leaflets, which possess two prominent abaxial stomatal grooves that are characteristic of the genus *Becklesia*. We

reassign three other French cycad fossils previously described under different generic names to *Becklesia*. Finally, we briefly discuss the geographical and stratigraphical implications of the genus and also consider presence of entire cycads in the fossil record.

Keywords : Cycads, *Becklesia*, Oxfordian, Upper Jurassic, Sarthe, NW France.

RÉSUMÉ

Les macrorestes de *Becklesia* Seward 1895 emend. Watson and Cusack 2005, un genre rare et éteint de cycadale, sont connus depuis plus d'un siècle en Grande-Bretagne et en Libye. Historiquement, ce genre à été mal caractérisée : plusieurs cycadales fossiles qui ressemblent à *Becklesia* ont été incluses dans d'autres genres comme *Cycadites* ou *Paracycas*. Nous décrivons ici une nouvelle espèce, *B. maulnyi* sp. nov., à partir d'un spécimen exceptionnel, presque complet, retrouvé dans les collections anciennes du Musée Vert du Mans. L'échantillon est constitué de l'apex d'une tige portant des feuilles pétiolées et pennées, des folioles fines et largement espacées, ainsi que deux sillons stomatiques caractéristiques du genre. Nous réattribuons également plusieurs cycadales françaises décrites précédemment sous d'autres noms au genre *Becklesia*. Enfin, nous discutons brièvement la répartition géographique et stratigraphique de ce genre, ainsi que de la présence de spécimens entiers de cycadales dans le registre fossile.

Mots-clés : Cycadales, *Becklesia*, Oxfordien, Jurassique supérieur, Sarthe, NW France.

1. Introduction

The genus *Becklesia* (Seward 1895) Watson and Cusack 2005 was created by Seward for the rare Berriasian aged (Early Cretaceous) cycad species *B. anomala* from the English Wealden. Seward's account was based on fragmentary fronds fragments that resembled those of extant cycads, but as documented by Seward, the genus was poorly characterised preventing its systematic relationships with other cycadalean plants from being determined. Watson (1969) established from the English Wealden a second species, *Becklesia sulcata*, for cycad leaf remains that include cuticular features, and Oldham (1976) identified *B. sulcata* as well as two further species that had similarity with *B. sulcata* from isolated cuticles also from the English Wealden. However, Watson et al. (2001) transferred Oldham's additional species to the non-cycad *Torreyites detriti* leaving only *B. anomala* and *B. sulcata* within the genus. Apart from these accounts from the English Wealden, the genus *Becklesia* has only been encountered in the Jurassic of Libya with Principi (1919) reporting *B. anomala* based on its distinctive morphology.

Based on the features of *Becklesia anomala* and *B. sulcata* Watson and Cusack (2005, p. 20) described in detail the leaf morphology and cuticle of the genus for the first time, emending the generic diagnosis as part of their monographic revision of English Wealden Cycads. They considered *Becklesia* to possess leaves with linear leaflets which are either simple or forked, and its cuticle has haplocheilic stomata organised in two parallel, longitudinal grooves on the abaxial surface of the pinna. However, Watson and Cusack's account is based on isolated leaves from which the organisation of the leaves on the plant is unknown, as are their fertile organs.

Here we describe a new species of *Becklesia* from the Jurassic of France based on a well-preserved specimen that represents the apex of a plant in which the leaves remain in organic attachment to the crown. We discuss the relevance of the entire nature of the crown in interpreting the plant organisation and habit. We also consider the presence of other fossil cycads in which well-preserved crowns are known from other stratigraphical intervals as well as the palaeogeographical and stratigraphical implications of the new species.

2. Material and methods

The sample MHNLM 2003.1.4962 studied here is housed in Musée Vert, natural history museum of Le Mans (Sarthe, NW France). The oldest label joined to the specimen (Fig. 1) indicates that it belonged to the "Cabinet de Maulny". Louis Maulny (1758-1815) was a naturalist of Le Mans, whose collection was bought by the museum of Le Mans after his death in 1816 (Delaunay, 1945). This first label has been written by Narcisse Desportes (1776-1856), curator of the museum between 1833 and 1856. It indicates with doubt the genus *Zamia* and the collection site in Écommoy (Sarthe, NW France) (Fig. 2). Two other labels on the specimen were written at the end of the 19th century and during the first part of the 20th century have copied the previous label and added no further information.

[Insert Figures 1 & 2 : First label of *B. maulnyi* sp. nov. / Localisation of Écommoy]

The unusual sediment of the studied specimen has been compared with the palaeontological collections housed in the Musée Vert in order to provide further information on its provenance. An ammonite (MHNLM 2003.1.4686) collected a few decades later (June 29, 1852) by the local palaeontologist Edouard Guéranger (1801-1895) from Ecommoy is preserved in a very similar rock matrix. It probably confirms the geographical origin written by Desportes and also helps to constrain the geological age.

The sediment for both the fossil plant and ammonite is a fine sandy and argillaceous, bicoloured, yellow and grey limestone. This fine grained sedimentary facies has preserved the mold of the fossil plant including grooves on the leaves but lacks cuticular preservation. This rock corresponds to the "Marnes et calcaires silteux de La Vacherie" [marl and silty limestone of La Vacherie], a local formation with terrestrial influence form the Lower Oxfordian aged *Mariae* zone and *Praecordatum* sub-zone (Manivit et al., 1988). Moreover, the ammonite is an unnamed small *Kranaosphinctes* that supports a Lower Oxfordian age corresponding with the end of the

Scarburgense sub-zone to the beginning of the *Praecordatum* sub-zone. In addition, a Cardioceratidae sampled by one of us (P. C.) a few years ago clearly indicate the *Praecordatum* sub-zone.

The exact location(s) of the outcrop where either the plant or ammonite were collected are unknown. However, following the first geological study of the Bélinois by Guillier (Guillier, 1875), two quarries were evident in the region, namely “La Vacherie” and “l’Épine”. These two quarries were approximately 1.5 km apart and both are now back filled. There are no Oxfordian aged outcrops in the Bélinois area today. However, a stratigraphic column of “La Vacherie” is provided by Guillier (1886, p. 178).

Specimen MHNLM 2003.1.4962 is an imprint of the lower face of a crown of leaves viewed from above and is preserved among poorly-preserved marine shelly fauna (Fig. 3A). It is also an outcast molding with relief and micro-relief able to preserve some architectural features. All the leaves are incomplete apically, but the lower-mid parts are more or less entire and are connected to the apex of the stem to form the crown (Fig. 3A). Five leaves are preserved; two of them bifurcate close to the insertion point with the crown. Small areas of a few of the leaflets are still covered by sediment protecting small and fragile carbonaceous remains that may be fusinized. They can perhaps in the future provide new details at cellular scale with an appropriate non-destructive method capable of studying these fragile remains *in situ*. Others small and unidentifiable plants fragments are also present on the sample.

The specimen was observed using a Leica EZ4 binocular microscope and macrophotography was undertaken using a Canon EOS700D with Canon EF-S60mm F2.8 Macro USM lens. Moreover, a petrological thin section (30 µm thick) was made from sample 2003.1.4962 to better characterize the geological context; it is housed in Musée Vert of Le Mans with the number MHNLM 2003.1.4962b.

3. Geological and palaeoenvironnemental context

The fossil described here occurred on the eastern border of the Massif Armorican, an old Hercynian massif widely flattened since the Lower Jurassic (Bessin et al., 2015). At this time, two main domains can be recognized in this area: the Normandy domain to the north and the Le Mans domain to the south, separated by an hydrodynamic barrier formed by the positive epeirogenic tendency of the Perche promontory (Dugué, 1989, 1991; Mégnien et al., 1980b). The locality of Écommoy is part of the natural region called Bélinois within the Le Mans domain.

The palaeoenvironment of the Bélinois is usually interpreted by comparison between the local “Marnes et Calcaires de la Vacherie” Formation and two better known formations, namely the “Marnes de Villers” Formation in the Normandy domain and the “Marnes à Pernes” Formation around the Perche promontory. They are dated to the *Mariae* zone (Lower Oxfordian) that corresponds to a major flooding event and then to a highstand system tract (HST) (Haq et al., 1987). Their classical interpretation is a relatively deep marine muddy platform (outer shelf), subject to some terrigenous influence with remains of terrestrial animals and wood washed into this setting (Mégnien et al., 1980a; Dugué, 1989).

An observation on the sediment in thin section of the specimen described here provides further data concerning the depositional environment. This sediment is a limestone with bimodal distribution between fine (less than 200 µm) particles that are dominant and biocorroded bioclasts including pelloids, and coarser particles that represent either fragmentary bivalves or *in situ* bivalves and gastropods with very thin shells. This lithology is classified as a packstone inside witch small pieces (<300 µm) of organic matter are common. The sediment is extensively bioturbated. The matrix and allochems in the packstone are suggestive of two different environmental conditions in which the overall texture of the packstone suggests relatively high energy conditions, whereas the biocorrosion, bioturbation and *in situ* thin shells suggest lower energy conditions.

Overall, the sediment suggests a marine depositional environment like a large embayment episodically supplied by bioclasts and terrestrial organic matter during storm and associated flood events (Guillier 1886, p. 178). The fossil plant described here is certainly a terrestrial component washed into the marine depositional setting. Judging by the completeness of the preserved cycad crown, the specimen has not been subjective to significant taphononic fragmentation due to transportation (e.g. Seilacher et al., 1985).

4. Systematic palaeontology

Order CYCADALES Persoon (1807)

Family UNCERTAIN

Genus ***Becklesia*** Seward (1895) emend. Watson & Cusack (2005).

***Becklesia maulnyi* sp. nov.**

Material and holotype. The holotype constitutes the only available material and corresponds to specimen MHNLM 2003.1.4962 housed in the Musée Vert of Le Mans, Sarthe, France.

Age and occurrence. Lower Oxfordian, Marnes et Calcaires Silteux de La Vacherie, Écommoy (Sarthe, NW France).

Etymology. The species epithet is derived from the surname of Louis Maulny, naturalist and first owner of the holotype.

Diagnosis. Leaves petiolate and pinnate with thin and widely separated leaflets. At least some leaves bifurcating near the base of the lamina, separated in two equal ramifications each similar to a simple leaf. Leaflets simple, linear-lanceolate, weakly decurrent, with rounded apex and inserted at an acute angle. Presence of two parallel longitudinal grooves separated by a wide and

flat central band occurring both in the rachis and leaflet on the abaxial surface.

Comment. The present species conforms well to the morphological features of *Becklesia* but lacks cuticular preservation that is inherent to the diagnosis of the genus. Rather than create a new genus for similar fossils in which cuticle is absent owing to the quality of preservation, we opt to establish a new species of *Becklesia*. This is based on its overall similarity with existing species that show they are closely related, and in particular the longitudinal grooves on the rachis and abaxial surface of the leaves are characteristic of the genus *Becklesia.* Consistent differences in the morphology of the leaves and leaflets and the absence of cuticular features in the present species do not allow us to place it within an existing species of the genus.

[Insert figures 3 & 4]

Description. The leaves are regularly disposed in a circle around a central depression positioned relative to the apex of the stem (Fig. 3A). Leaves are petiolate, pinnate and they sometimes fork near the insertion point on the stem that divides the leaf into two ramifications (Figs. 3B-C, 4A). Individual leaves / ramifications are up to 125 mm long but are each incomplete such that their entire length would have been longer. Where leaves fork the two ramifications have approximately the same shape and each has the same structure and organisation than the single (non-ramified) leaves. The angle between individual leaves or between two ramifications on a single leaf is approximately 45° except one that is 90° (Fig. 3A) from which the presence of simple leaves may in some cases be due to incomplete preservation.

The length of the petiole is less than 28 mm; at its top some small bumps replace the first leaflets (Fig. 3D). These bumps resemble spines on petioles of extant armed cycads. The rachis and the petiole are flat and their width, about 2 mm (1.7-2.1 mm), is more-or-less constant over their entire length. The imprint of the abaxial face shows in sub-marginal position two linear bulges that are Ω-shaped in transverse section (Figs. 3D, 4B-D). These bulges are about 0.2 mm wide and are separated by a wide and flat band of about 1.2 mm. The bulges follow the lateral margin in both the

rachis and leaflets, and thus bypass the flat band of each leaflet. The bulges correspond favourably with the mould of stomatal grooves that have been filled with sediment and the flat area between them to a non-stomatal band in fossil cycads.

The leaflets are simple, linear-lanceolate with an entire margin, rounded apex and are at an angle of about 60-65° to the rachis typically with an opposite to sub-opposite arrangement but sometimes irregular (Figs. 3A, E-F). Leaflet basiscopic margin is decurrent and acroscopic margin is lightly expended (Fig. 3F). Their length is up to 28 mm and their width is constant, at about 2 mm (1.7-2.1 mm). Individual leaflets are separated from each other by 2-4 mm, rarely more. The basal leaflets are shorter than the middle leaflets and the length of the upper leaflets decrease (but leaflet apex is rarely preserved). The imprint of the abaxial face shows two parallel and longitudinal Ω-sharped bulges in sub-marginal position that correspond to the position of stomatal grooves. Stomatal grooves are about 0.3 mm wide (Figs. 3F, 4C-D) and are also separated by a flat band of about 0.5 mm width which corresponds to the non-stomatal area. At the apex of a leaflet, the two grooves converge quickly and merge. Features of the cuticle are unknown.

Comparison with others species. The genus *Becklesia* is primarily based on the two parallel and longitudinal stomatal grooves on the abaxial face of leaflets and features of the cuticle. The cuticle is not preserved in our sample due to preservational limitations, but this kind of longitudinal groove is a unique characteristic of cycad-like foliage (Watson and Cusack, 2005). This rare and unmistakable trait argues in favour of this generic attribution, as does the relative temporal (Oxfordian / Berriasian) and palaeogeographical proximity to other localities in which *Becklesia* occurs in SE England and NW Libya.

The specimen described here differs in some ways from others species of *Becklesia*. The dimensions of the leaves, rachis and leaflets of *Becklesia anomala* are larger than those of our sample. Likewise, the leaflet apices of *B. anomala* and *B. sulcata* are acute and the two stomatal

grooves are non-convergent, contrary to our specimen where they are respectively round and convergent. Finally, leaflets do not bifurcate in the French specimen unlike *B. anomala* (Watson and Cusack, 2005), the only other species in which macro-remains are known for comparison. Moreover, the forking leaves seem to be a specific feature of the French specimen but that represents a preservational limitation in the other species in which the crown is unknown. Although the French specimen lacks cuticle, the stomatal grooves demonstrate their presence and in this regard it is also similar to those of *Becklesia*.

Three French cycad species from the Upper Kimmeridgian of the Jura mountains are morphologically similar to *Becklesia* but are currently placed within different genera. We re-evaluate these species in light of the findings of Watson and Cusack (2005) and the present investigation on the organisation and distribution of *Becklesia*. However, we will not describe these species again as their previous accounts are as detailed as the materials permit.

Cycadites lorteti as described by Saporta (1875) and emended by Barale (1981, pp. 69–71) has two characteristic longitudinal grooves on the rachis corresponding to the stomataliferous grooves in *Becklesia*. *C. lorteti* differs from *B. maulnyi* sp. nov. in having larger leaflets (2.5–4 x 30–115 mm), its leaflet apices being acute rather than rounded, and the narrower width of its rachis (9 mm near the basal part). Historically, all Mesozoic leaves which had a superficial resemblance with those of the modern genus *Cycas* have been placed within the genus *Cycadites* where features that would allow a more accurate generic determination to be made are unavailable. Stomatal grooves allow us to place this species within *Becklesia* for which they are distinctive features. We therefore transfer *C. lorteti* into *Becklesia lorteti* comb. nov.

Paracycas sp. A as described by Barale (1981, pp. 65–68) possesses two longitudinal grooves in the same position as observed in *Becklesia.* This species possesses a cuticle that comprises haplocheilic stomata born in two parallel rows separated by a non-stomatal band. However, *P*. sp. A differs from *B. maulnyi* in having a greater spacing between leaflets (10-15 mm) and having a less acute insertion angle on leaflets (about 90°), but the width of rachis and

dimensions of the leaflets dimensions are similar in the two species. *Paracycas* was established by Harris (1964) for fossils with cycads-like cuticular features and only one median vein. Harris' diagnosis of *Paracycas* lacks mention of stomatal furrows. The features of *P.* sp. A of Barale (1981) are consistent with those of *Becklesia* into which the species should be transferred as *Becklesia* sp. A.

Paracycas sp. B of Barale (1981) lacks cuticle but differs from *B. maulnyi* sp. nov. mainly in the width of the rachis (4–7 mm) and leaflets (3–4 mm at their base), but this species is based on too fragmentary remains which precludes more detailed comparisons. Considering its occurrence with other species of *Becklesia* rather than *Paracycas*, we conclude that this species more likely belongs within the genus *Becklesia* to which it should be transferred as *Becklesia* sp. B.

5. Growth habit and environmental implications of *Becklesia maulnyi* sp. nov.

Becklesia maulnyi sp. nov. probably had a short subterranean trunk and an herbaceous habit if we consider the short diameter of the central hole and the low number of leaves in the studied sample: this shape of trunk exists in 6 of 11 genera of modern cycads (Whitelock, 2002). However, we cannot exclude a palm-like habit, especially if the specimen was ontogenetically young. A few cycad species with subterranean trunks stock water in their roots which tend to be succulent and tuberous (Whitelock, 2002), but this shape exist both in drought-tolerant (*Ceratozamia microstrobila, C. zaragozae, Encephalartos caffer, E. cerinus, E. cupidus, E. humilis, Macrozamia glaucophylla, Stangeria eriopus*) and moisture-tolerant cycads (*Bowenia spectabilis, Ceratozamia hildae, C. kuesteriana, C. miqueliana, C. withlockiana, Encephalartos villosus, Zamia splendens, Z. variegata*) and thus cannot be considered exclusively as a xeromorphic feature.

Longitudinal stomatal grooves specific to *Becklesia* are a xeromorphic feature confirmed by the localisation of trichome cells on the border of the grooves in *B. anomala* (Watson and Cusack, 2005). However, the protection of stomata does not exclusively occur in dry climates, but equally in environments with high water availability: a drop of liquid water can sometimes occlude

the stomatal aperture and so inhibit the respiratory function if the stoma is non-protected (Haworth and McElwain, 2008). However, in coastal environments sea spray affects plants in their water regulation in a similar way to drought, so similar adaptations are used in both cases to defend against water loss. A structure close to longitudinal stomatal grooves of *Becklesia* is known from an extant member of the Poaceae, *Ammophila arenaria,* that lives in coastal settings (Konlechner and Hilton, 2009). In *Ammophila* leaves roll on themselves to form a stomatal cavity that is elongated along the longitudinal axis of the leaf. Many digitations of the stomatal epidermis increase also the respiratory surface. Even if this last structure is more elaborate than the longitudinal stomatal grooves of *Becklesia*, the principle is the same: an elongated cavity, open only through a slit, protects the stomatal area to external environment and increase resistance against desiccation. Desiccation can be due to sea spray at least in the case of this beach grass, but probably also in *Becklesia* too.

The leaf morphology of *B. maulnyi* sp. nov. with its widely spaced leaflets reflects a double adaptation: wind resistance of the plant is improved by increasing the spacing of the leaflets, and the consecutive reduction of the leaf surface attenuates also its evapotranspiration, especially in a context of high light intensity. In contrast, that excludes any environment where interspecific competition for light is strong, so its environment is probably a relatively open one. Moreover, the presence of two ramifications halves the length of the leaves at a constant photosynthetic surface and thus, protects the plant against wind damage. As a consequence, the living area of this plant was probably an open environment with strong wind and light, coherent with an herbaceous habit and adaptations against desiccation.

From our interpretations we consider likely that *Becklesia maulnyi* sp. nov. lived in close proximity to the sea in a coastal setting and that it lived in an open, windy and sunny growth environment. Coastal dune ridges satisfy these conditions and represent a likely growth environment. In coastal dune ridges the sandy soil is unstable and regularly mobilized and re-worked by wind. Moreover, some dune plants use this for their vegetative reproduction and

dispersal strategy (Konlechner and Hilton, 2009). In the Jurassic, floras characteristic of dune ridges are totally unknown because dune ridges do not offer good conditions for plant fossilization; they comprise freely draining sandy substrates that allow plant materials to oxidize and decay rather than be preserved. Moreover, current dune ridge floras cannot be used as a model on which to base Jurassic plant distributions as present day dune floras mainly comprise flowering plants that did not exist during the Jurassic. In the absence of angiosperms, this environment was probably colonized by other groups of plants potentially including cycads.

On the other hand, the strong environmental stress of extant dune plants must be close to those of Jurassic ones as the same physical factors are unchanged through time. Plants growing in dune ridges must deal with environmental stresses from salt spray, sand burial, swash inundation, dryness, high light intensity, wind exposure, soil salinity and nutrient deficiency (Hesp, 1991). The comparison between our sample features, actual and fossil cycad characteristics, and response to environmental stress of modern dune plants can help to sustain an origin of *B. maulnyi* sp. nov. in a dune ecosystem. Among the factors described above, *B. maulnyi* sp. nov. shows evidence of adaptation to dryness, high light intensity and wind exposure in the unique form of its leaves and stomatal grooves. Furthermore, protection against salt spray and dryness is reinforced by the comparison between the rolled leaves of the beach grass *Ammophila arenaria* (Konlechner and Hilton, 2009) and the longitudinal stomatal grooves of *Becklesia*. Protection against sea spray and soil salinity can be equally inferred by comparison with *Becklesia anomala* that had potential salt glands on both sides of its leaflets (Watson and Cusack, 2005). While the majority of extant cycads are not tolerant to salt, some living species occur in coastal environments including species of *Cycas*, *Dioon*, *Encephalartos*, *Macrozamia* and *Zamia* where they are able to deal with the physiological consequences of soil salinity and sea spray. For example, extant *Zamia roezlii* occurs in coastal marshes occasionally inundated at high tide with seawater, differing significantly from most other cycads that generally prefer well drained habitats (Whitelock, 2002).

More generally, cycads as a group have a number of strengths to successfully establish

themselves in severely stressed ecosystems such as dune ridges: their subterranean rooting system is often tuberous and succulent (Whitelock, 2002) and the medullar parenchyma of the stem is very developed at least in all arborescent cycads. These adaptations confer the ability to stock water and thus to protect the plant from periods of water stress. Moreover, many extant cycads are nitrogen fixers *via* a symbiosis with cyanobacteria (*Nostoc* sp. and others) through specialized coralloid roots. Coralloid roots allow cycads to live in an almost sterile soil, like those of mineral rich coastal dunes where organic matter is limited. Their nitrogen autotrophy is especially important because this element is the main limiting factor for plant growth in dune ecosystems (Hesp, 1991). Otherwise, some living cycads with a subterranean trunk have roots with contractile capabilities able to pull the stem into the ground (Whitelock, 2002); maybe some fossil cycads with a comparable capacity can withstand episodic sand burial in dune ecosystems.

However, no potential adaptation is recognized in *B. maulnyi* sp. nov. or in other extant or fossil cycads to deal with swash inundation, but we consider that *B. maulnyi* sp. nov. has potential adaptations to each other major stress factor of the dune ecosystems cited by Hesp (1991), either directly observed or as inferred above. The hypothesis that *B. maulnyi* sp. nov. inhabited a coastal dune environment is impossible to demonstrate directly because this plant has been transported into an adjacent marine depositional setting, potentially following swash inundation. Nevertheless, the conjunction of many adaptations coherent to a growth in a coastal dune ecosystem and the transport of a near whole plant with attached leaves into a relatively deep submarine mudflat can be easily explained only if the fossil plant came from a coastal environment under strong erosion at the scale of its lifetime. A coastal dune ecosystem corresponds well to this interpretation.

6. Taphonomic and palaeobiogeographic considerations

The taphonomic process at the origin of this fossil is probably original, perhaps unique, because it allowed the preservation of a leafy crown in an unambiguous marine environment, arranged to strongly suggest a life position. That involves transportation of at least the upper part of

the trunk, and maybe even the whole plant from its growth environment, or perhaps the flooding of a formerly terrestrial environment, or rapid burial of the trunk up to the level of the lamina. If only the upper part of the trunk was transported, this means that it was previously detached from the rest of the plant, or the entire plant could have been uprooted. Detaching the crown of a cycad or uprooting the entire plants could conceivably be achieved by wind, flooding or animal action. As the leaves remain attached to the plant and are relatively complete with little damage, transportation distances and energy levels were unlikely to have been high for which more damage and fragmentation would be expected.

As well as *Becklesia maulnyi* sp. nov. other examples or entire cycad crowns are known from the fossil record including *Leptocycas gracilis* from the Triassic of North America (Delevoryas and Hope, 1971), *Holozamites hongtaoi* (X. Wang et al., 2009) and *Leptocycas yangcaogouensis* (Zhang et al., 2010) from the Upper Triassic of China. These accounts demonstrate consistent crown morphology with modern cycads and *B. maulnyi* sp. nov., show conservatism in form from fossil and living cycads, and emphasize that entire cycads crowns are increasingly common in the fossil record. As far as we are aware, taphonomic studies have not been conducted on these other entire cycads. Such kinds of fossils, for example entire Palaeozoic aged Noeggerathialean ferns, are typically considered to represent preservation of in-situ plants preserved in their growth environments under obrution (rapid burial) deposits such as volcanic ash fall horizons (e.g. J. Wang et al., 2009). *B. maulnyi* sp. nov. is different as it is clearly preserved in a marginal marine setting as evidence by the lithological features of the host rock, and is not *in-situ* in a terrestrial context.

[Insert figure 5 - Position of Mesozoic outcrops with *Becklesia* remains.]

Despite being established more than a hundred years ago, species of *Becklesia* are very rare among Mesozoic floras, and where they are present they are represented by one to a few individual specimens in each of the English, Libyan or French Jura and Écommoy assemblages in which they occur. However, the spatio-temporal distribution of this genus shows an interesting

pattern: all known Jurassic species come from France, but the Cretaceous species seem more dispersed with southern English and northern Libyan occurrences (Fig. 5). However, the very sparse data prevent further analysis of the origin and dispersion of *Becklesia*.

Acknowledgements

The authors thank Patrice Raboeuf, technician at Musée Vert of Le Mans, to have found in the collections the ammonite which has probably strengthened the dating, and Xavier Le Coz, technician in Géosciences Rennes for making the thin section. We thank J. Dejax and an anonymous reviewer for the constructive remarks of an earlier version of the manuscript.

References

Barale, G., 1981. La paléoflore jurassique du Jura français : Étude systématique, aspects stratigraphiques et paléoécologiques. Documents des laboratoires de géologie de Lyon 81, 467 p.

Bessin, P., Guillocheau, F., Robin, C., Schroëtter, J.-M., Bauer, H., 2015. Planation surfaces of the Armorican Massif (western France): Denudation chronology of a Mesozoic land surface twice exhumed in response to relative crustal movements between Iberia and Eurasia. Geomorphology 233, 75–91.

Delaunay, P., 1945. Louis Maulny, naturaliste et collectionneur (1758-1815). Ses amis, ses disciples, son temps, ses successeurs. Bulletin de la Société d'agriculture, sciences et arts de la Sarthe 60, 1–132.

Delevoryas, T., Hope, R.C., 1971. A new Triassic cycad and its phyletic implications. Postilla 150, 1–21.

Dugué, O., 1989. Géodynamique d'une bordure de massifs anciens. La bordure occidentale du bassin anglo-parisien au Callovo-Oxfordien. Pulsations épirogéniques et cycles eustatiques

PhD Thesis University of Caen, 93 p. (unpublished).

Dugué, O., 1991. Comportement d'une bordure de massif ancien et cortèges de minéraux argileux : l'exemple de la bordure occidentale du Bassin Anglo-Parisien au Callovo-Oxfordien. Palaeogeography, Palaeoclimatology, Palaeoecology 81, 323–346.

Guillier, A., 1875. Note géologique sur le Bélinois. Bulletin de la Société d'agriculture, sciences et arts de la Sarthe 15, 59–69.

Guillier, A., 1886. Géologie du département de la Sarthe. Monnoyer, Le Mans, 430 p.

Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–1166.

Harris, T. M., 1964. The Yorkshire Jurassic flora. II. Caytoniales, Cycadales & Pteridosperms. British Museum, London, 191 p.

Haworth, M., McElwain, J., 2008. Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. Palaeogeography, Palaeoclimatology, Palaeoecology 262, 79–90.

Hesp, P., 1991. Ecological processes and plant adaptations on coastal dunes. Journal of Arid Environments 21, 165–191.

Konlechner, T.M., Hilton, M.J., 2009. The potential for marine dispersal of *Ammophila arenaria* (Marram grass) rhizome in New Zealand. Journal of coastal research. Special Issue 56, 434–437.

Manivit, J., Lablanche, G., Depagne, J., 1988. Notice explicative, carte géologique de la France (1/50 000), feuille Marquise (5). Bureau de recherches géologiques et minières, Orléans.

Mégnien, C., Mégnien, F., Alcaydé, G., Allouc, J., Amédro, F., Autran, A., Barta, L., Bignot, G., Blondeau, A., Bonte, B., Cariou, É., Cavelier, C., Celet, P., Corsin, P., Courel, L., Debrand-Passard, S., Demassieux, L., Durand, M., Fauvel, P.-J., Fily, G., Foucher, J.-C., Geisler, D., Hanzo, M., Juignet, P., Kuntz, G., Laurain, M., Laurin, B., Lautridou, J.-P., Leplat, J., Le Roux, J., Lorenz, C., Lorenz, J., Louail, J., Maget, P., Magniez, F., Manivit, J., Marchal, C.,

Marchand, D., Médioni, R., Ménillet, F., Menot, J.-C., Monciardini, C., Mouterde, R., Muller, A., Pareyn, C., Pascal, A., Perreau, M., Pomerol, B., Pomerol, C., Rasplus, L., Rat, P., Renard, M., Rioult, M., Riveline, J., Robaszynski, F., Salomon, J., Thierry, J., Tintant, H., Tourenq, J., Voisin, L., Wyns, R., 1980a. Synthèse Géologique du Bassin de Paris. III - Lexique des noms de formations. Mémoires du BRGM 103, 467 p.

Mégnien, C., Mégnien, F., Alcaydé, G., Bignot, G., Blondeau, A., Cavelier, C., Courel, L., Debrand-Passard, S., Enay, R., Juignet, P., Labourguigne, J., Magniez, F., Médioni, R., Monciardini, C., Rioult, M., Salomon, J., Thierry, J., Tintant, H., Allouc, J., Amédro, F., Autran, A., Barta, L., Cariou, É., Debeglia, N., Destombes, P., Donsimoni, M., Dubois, P., Durand, M., Fauvel, P.-J., Feys, R., Fily, G., Gabilly, J., Greber, C., Hanzo, M., Laurain, M., Laurin, B., Lefavrais-Raymond, A., Leplat, J., Le Roux, J., Lorenz, J., Louail, J., Maget, P., Maiaux, C., Manivit, J., Marchal, C., Marchand, D., Ménillet, F., Menot, J.-C., Pareyn, C., Perreau, M., Pomerol, B., Pomerol, C., Rasplus, L., Riveline, J., Robaszynski, F., Russel, D.E., Sornay, J., Tourenq, J., Wyns, R., Yapaudjian, L., 1980b. Synthèse Géologique du Bassin de Paris. I - Stratigraphie et paléogéographie. Mémoires du BRGM 103.

Oldham, T., 1976. Flora of the Wealden plant debris beds of England. Palaeontology 19, 437–502.

Persoon, C.H., 1807. Synopsis plantarum, seu enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum. Pars Secunda. Paris, 657 p.

Principi, P., 1919. Filliti wealdiane della Tripolitania. *in* : Zaccagna, D. Itinerari geologici nella Tripolitania Occidental. Memorie descrittive della Carta Geologica d'Italia 18, 71-85.

Saporta, G. de, 1875. Paléontologie française ou description des fossiles de France. 2^{e} série – Végétaux. Plantes Jurassiques. Tome II. Cycadées. Masson, Paris, 352 p.

Seilacher, A., Reif, W.-E., Westphal, F., 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. Philosophical Transactions of the Royal Society B 311, 5–23.

Seward, A., 1895. Catalogue of the Mesozoic plants in the department of Geology, British Museum (Natural History). The Wealden flora. Part II. Gymnospermae. London, 259 p.

Wang, J., Pfefferkorn, H.W., Bek, J., 2009. Paratingia wudensis sp. nov., a whole Noeggerathialean plant preserved in an earliest Permian air fall tuff in Inner Mongolia, China. American Journal of Botany 96, 1676–1689.

Wang, X., Li, N., Wang, Y.D., Zheng, S.L., 2009. The discovery of whole-plant fossil cycad from the Upper Triassic in western Liaoning and its significance. Chinese Science Bulletin 54, 3116–3119.

Watson J., 1969. A Revision of the English Wealden Flora, I. Charales-Ginkgoales. Bulletin of the British Museum (Natural History) Geology 17, 207–254.

Watson, J., Cusack, H., 2005. Cycadales of the English Wealden. Palaeontographical society, London, 189 p.

Watson, J., Lyndon, S.J., Harrison, N.A., 2001. A revision of the English Wealden flora. III. Czekanowskiales, Ginkgoales & allied Coniferales. Bulletin of the British Museum (Natural History). Geology. 57, 29–82.

Whitelock, L.M., 2002. The Cycads. Timber press, Portland, Oregon, 374 p.

Zhang, J.W., Yao, J.X., Chen, J.R., Li, C.S., 2010. A new species of *Leptocycas* (Zamiaceae) from the Upper Triassic sediments of Liaoning Province, China. Journal of Systematics and Evolution 48, 286–301.

Fig. 1. First Label of *Becklesia maulnyi* sp. nov.

Premier cartouche de Becklesia maulnyi *sp. nov.*

Fig. 2. Position of Écommoy on a simplified map of NW France.

Emplacement d'Écommoy sur une carte simplifiée du NO de la France.

Fig. 3. General and detailed views of *Becklesia maulnyi* sp. nov. A. General view of *B. maulnyi* sp. nov. B-C. Detailed view of the central depression relative to the apex of the stem. The arrow indicates two leaves that fork at the base, and the asterisk shows the leaf base shown in C. A and B have the same orientation. C follows the conventional orientation of a leaf; the sample is inclined to have the basal fork in a single focal plane. D. Detailed view of the upper part of the rachis of a bifurcated leave, after the basal fork. Arrow indicates the bumps that replace some of the first leaflets that appear to represent spines of extant armed cycads. E. View of the opposite to sub-opposite insertion mode of the leaflets. Arrow indicates one example of preserved carbonaceous (fusinized?) remain. F. Detailed view of some of the shorter (basal) leaflets showing the rounded apex and the bulge corresponding to the two stomatal grooves. The stomatal grooves converge quickly and merge at the apex of the leaflets. Arrows show the decurrent nature of the leaflets.

Vue globale et détaillée de Becklesia maulnyi *sp. nov. A. Vue globale de* B. maulnyi *sp. nov. B-C. Vues détaillées de la dépression centrale situé au niveau de l'apex de la tige. Les flèches indiquent deux feuilles bifurquées dès leur base, et l'astérisque la base de feuille détaillée en C. A et B ont la même orientation. C suit l'orientation conventionnelle d'une feuille ; l'échantillon est incliné pour présenter la bifurcation basale dans le même plan de mise au point. D. Vue détaillée de la partie supérieure du rachis d'une feuille bifurquée après la dichotomie basale. Les flèches indiquent les bosses qui remplacent les premières folioles et peuvent être comparées aux épines des cycadales armées actuelles. E. Vue du mode d'insertion opposé à sub-opposé des folioles. La flèche indique*

un exemple de reste charbonneux (fusinisé ?) préservé. F. Vue détaillée de quelques folioles très courtes (basaules) montrant l'apex arrondi et le renflement correspondant aux deux sillons stomatiques. Ceux-ci convergent rapidement et fusionnent à l'apex des folioles. Les flèches montrent la décurrence des folioles.

Fig. 4. Hypothetical reconstruction of some part of *Becklesia maulnyi* sp. nov. A. Reconstruction of the gross morphology of one leaf. The leaf length is based on the hypothesis than the longest leaf of the original fossil would be nearly complete. The "accidental" intercalary insertion of a leaflet at the base of the right ramification is intentional and corresponds to the leaf imprint shown on the right of Fig. 3A. B-C. Block-diagram of hypothetical reconstruction of transverse section of rachis (B) and leaflets (C). The stomatal grooves are not exactly in the same position in rachis and leaflet. D. Reconstruction of the position of the stomatal grooves (dark gray) on the abaxial leaf surface.

Reconstruction hypothétique de plusieurs partie de Becklesia maulnyi *sp. nov. A. Reconstruction de la morphologie globale d'une feuille. La longueur de celle-ci est basée sur l'hypothèse que le fragment le plus long préservé sur l'échantillon d'origine serait presque complet. L'insertion intercalaire « accidentelle » d'une foliole à la base de la ramification de droite est intentionnelle et correspond à l'empreinte de la ramification située à droite sur la Fig. 3A. B-C. Reconstruction hypothétique de la section transversale du rachis (B) et d'une foliole (C) sous forme de bloc-diagrammes. Les sillons stomatiques ne sont pas exactement au même emplacement dans ces deux cas. D. Reconstruction de l'emplacement des sillons stomatiques (gris foncé) sur la face abaxiale des feuilles.*

Fig. 5. Position of Mesozoic outcrops with *Becklesia* remains.

Localisation des gisements mésozoïques à Becklesia.

Figure 1

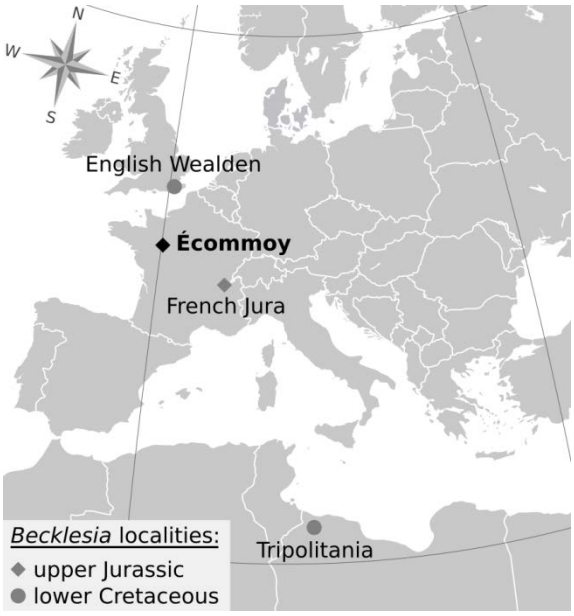

Figure 2

Figure 3.

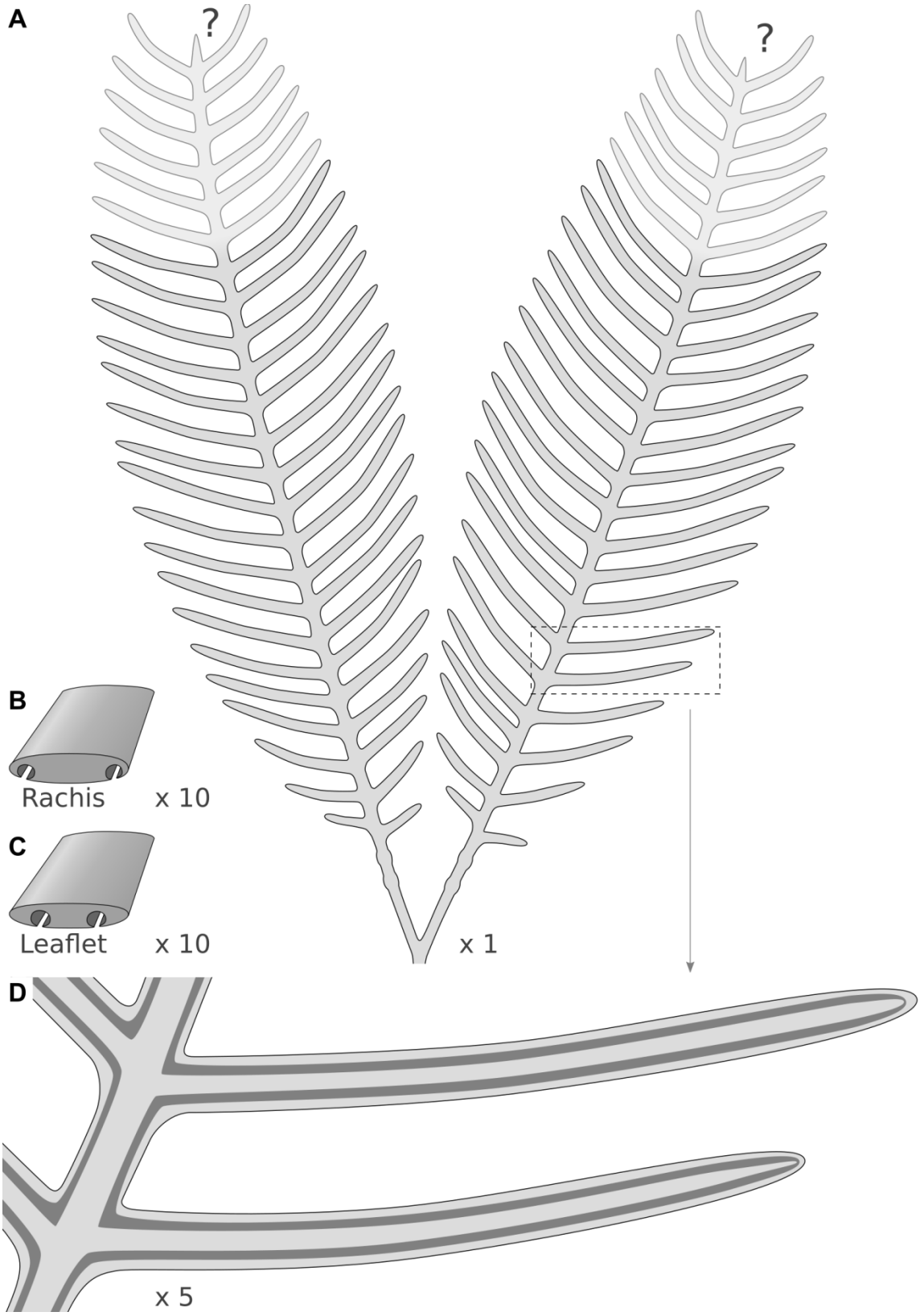

Figure 4

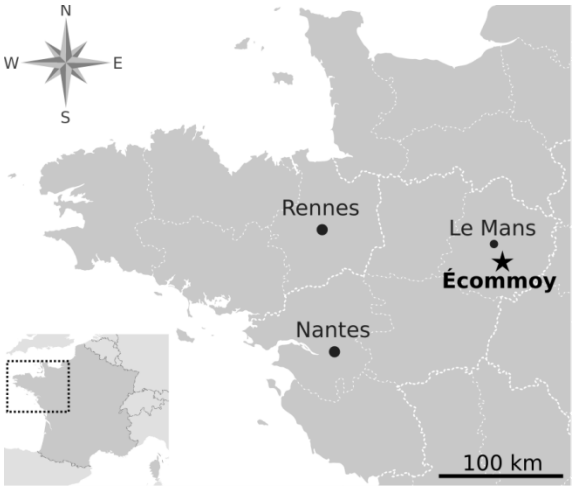

Figure 5